
Nomenclatural Changes of Some Californian *Castilleja* (Scrophulariaceae)

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ABSTRACT. In anticipation of the upcoming revision of the *Jepson Manual of the Flowering Plants of California*, the following 10 new nomenclatural combinations of Californian *Castilleja* subg. *Castilleja* at the subspecific level are proposed: *C. affinis* subsp. *litoralis* (Pennell) Chuang & Heckard, *C. affinis* subsp. *neglecta* (Zeile) Chuang & Heckard, *C. applegatei* subsp. *disticha* (Eastwood) Chuang & Heckard, *C. applegatei* subsp. *martinii* (Abrams) Chuang & Heckard, *C. applegatei* subsp. *pallida* (Eastwood) Chuang & Heckard, *C. applegatei* subsp. *pinetorum* (Fernald) Chuang & Heckard, *C. hispida* subsp. *brevilobata* (Piper) Chuang & Heckard, *C. lanata* subsp. *hololeuca* (Greene) Chuang & Heckard, *C. minor* subsp. *spiralis* (Jepson) Chuang & Heckard, and *C. subinclusa* subsp. *franciscana* (Pennell) Chuang & Heckard. The justification for these nomenclatural changes is briefly summarized.

The genus *Castilleja*, especially subgenus *Castilleja*, is notorious for its taxonomic difficulty, which is due at least partly to natural hybridization and associated polyploidy. We recently proposed to subdivide the expanded genus *Castilleja* into three subgenera (Chuang & Heckard, 1991): subgenus *Colacus*, with three sections, *Oncorhynchus*, *Pilosae*, and *Pallescentes*, to include bee-pollinated plants with bracts and calyx colored other than red and a relatively well-developed lower corolla lip, usually with some pouch development; subgenus *Gentrya*, a monotypic taxon from the Sierra Surutato of northern Sinaloa, Mexico, which exhibits a distinctive curved corolla and is probably also bee-pollinated; and subgenus *Castilleja*, comprising the majority of the species, which have a flower basically modified for hummingbird pollination, with bract and calyx tips predominantly red, a well-developed corolla tube, an upper lip much longer than the lower, and a lower lip reduced to three small teeth and lacking any pouch.

The purpose of this paper is to make appropriate nomenclatural changes in Californian *Castilleja* subg.

Castilleja in anticipation of the upcoming revision of the *Jepson Manual of the Flowering Plants of California* (Jepson, 1925). The following 10 new combinations are proposed at the subspecific level. This study is based on field observations and collections of *Castilleja* in California during the past two decades and abundant herbarium specimens deposited at CAS, JEPS, and UC.

1. ***Castilleja affinis*** Hooker & Arnott subsp. ***litoralis*** (Pennell) Chuang & Heckard, comb. nov. *Castilleja litoralis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 183. 1947. *Castilleja wightii* Elmer subsp. *litoralis* (Pennell) Munz, Aliso 44: 98. 1958. TYPE: U.S.A. Oregon: Coos County, Bandon, 19 July 1931, Pennell 15651 (holotype, PH).
2. ***Castilleja affinis*** Hooker & Arnott subsp. ***neglecta*** (Zeile) Chuang & Heckard, comb. et stat. nov. *Castilleja neglecta* Zeile in Jepson, Man. Fl. Pl. Calif. 936. 1925. TYPE: U.S.A. California: Marin County, Tiburon, 7 July 1907, Brandegees s.n. (holotype, JEPS).

Castilleja affinis is a highly intractable polyploid complex, which has six levels of polyploidy, ranging from $n = 12$ to 72 (Heckard, 1968; Chuang & Heckard, unpublished data). Pennell (1951) recognized six species in the *C. affinis* complex. These species (*C. affinis*, *C. californica* Abrams, *C. douglasii* Benthams, *C. inflata* Pennell, *C. litoralis*, and *C. neglecta*) were placed in four different sections of the genus on the basis of such morphological features as shape of leaf and calyx lobes, and the pubescence of the upper corolla lip (beak). There is too much variability and overlap in these features within the group to delimit satisfactorily distinct species. Some populations might warrant subspecific recognition but do not necessarily coincide with polyploidy levels, and various polyploidy levels intergrade to such an extent that it is impossible to make a useful taxonomic separation. Furthermore, *Cas-*

tilleja affinis itself is not sharply delimited from neighboring species, either because of its probable partial origin from them in the past or because of more recent hybridizations with them. Therefore, taxonomic recognition of any entities other than the three subspecies, subspecies *affinis*, subspecies *litoralis*, and subspecies *neglecta*, seems impractical. The taxonomic difficulties of the *C. affinis* complex are comparable to those in the Californian component of such other complex species as *Dactylis glomerata* Linn. (Stebbins & Zohary, 1959), *Ambrosia dumosa* (A. Gray ex Torr.) Payne (Raven et al., 1968), *Eriophyllum lanatum* (Pursh) Forbes (Mooring, 1975), and *Epilobium* [*Zauschneria*] *canum* (Greene) Raven (Raven, 1977).

Castilleja affinis subsp. *affinis* ($n = 12, 24, 36, 48$) is widespread over much of cismontane California at lower elevations in sandy and rocky soil in chaparral and coastal scrub. It is generally characterized by bristly puberulent herbage, 3- to 5-lobed leaves, acute bract and calyx lobes, and larger (25–40 mm), scarlet to orange-red flowers. A coastal-bluff form (Pt. Reyes Peninsula south to northern Santa Cruz) with rather fleshy leaves, distally inflated calyx, and less protruding corolla beak has been named *C. inflata* (= *C. wightii* subsp. *inflata* (Pennell) Munz). Another coastal sand-dune form (San Luis Obispo and Santa Barbara counties) has variable branched hairs in the herbage; this form has been named *C. affinis* var. *contentiosa* (J. F. Macbride) Bacigalupi, which perhaps represents a past introgressant between *C. affinis* and *C. mollis*. *Castilleja affinis* subsp. *litoralis* ($n = 48, 60, 72$) is distributed on coastal bluffs from northern California to northern Oregon. This subspecies is distinguishable by its usually glabrous herbage, entire leaves, obtuse to rounded bract and calyx lobes, and larger (25–40 mm), scarlet to orange-red flowers. *Castilleja affinis* subsp. *neglecta* ($n = 36$) is a rare serpentine endemic found only on Tiburon Peninsula and south of Nicasio Reservoir in Marin County and American Canyon in Solano County, and is characterized by its bristly puberulent herbage, 3- to 5-lobed leaves, acute bract and calyx lobes, and smaller (18–22 mm), yellow flowers.

3. *Castilleja applegatei* Fernald subsp. **disticha**

(Eastwood) Chuang & Heckard, comb. et stat. nov. *Castilleja disticha* Eastwood, Proc. Calif. Acad. Sci. III. 2: 289. 1902. TYPE: U.S.A. California: Fresno County, Converse Basin, South Fork of King's River, 1–3 July 1899, *Eastwood s.n.* (holotype, CAS).

Castilleja quibellii Beane, Contr. Dudley Herb. 4: 37. 1950. TYPE: U.S.A. California: Fresno County,

Rancheria Camp Ground, 11 July 1949, *Beane 1536* (holotype, DS; isotype, JEPS).

4. *Castilleja applegatei* Fernald subsp. **martinii**

(Abrams) Chuang & Heckard, comb. et stat. nov. *Castilleja martinii* Abrams, Bull. S. Calif. Acad. Sci. 1: 69. 1902. TYPE: U.S.A. California: Los Angeles County, Wilsons Peak, San Gabriel Mountains, 10 July 1901, *Abrams 1881* (holotype, DS; isotype, DS).

Castilleja clokeyi Pennell, Proc. Acad. Nat. Sci. Philadelphia 89: 420. 1937. *Castilleja martinii* var. *clokeyi* (Pennell) N. Holmgren, Mem. New York Bot. Gard. 21: 55. 1971. TYPE: U.S.A. Nevada: Clark County, Charleston Mountains, 8 July 1936, *Clokey & Clokey 7322* (holotype, PH; isotypes, BRY, CAS, DS, MO, NY, ORE, OSC, RSA, SD, UC, US, UTC, WTU).

Castilleja roseana Eastwood, Leaf. W. Bot. 2: 104. 1938. TYPE: U.S.A. California: Monterey County, between San Lucas and Priest Valley, 11 May 1936, *Eastwood & Howell 2460* (holotype, CAS; isotypes, CAS, GH, RSA).

Castilleja hoffmannii Eastwood, Leaf. W. Bot. 3: 116. 1942. TYPE: U.S.A. California: Ventura County, between Chula Vista Camp and summit of Mount Pinos, 26 May 1928, *Howell 3840* (holotype, CAS).

Castilleja gyroloba Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 186. 1947. TYPE: U.S.A. California: Los Angeles County, near Oak Flat Camp, 18 Apr. 1940, *Pennell 25140* (holotype, PH; isotypes, DS, GH, NY, PH).

Castilleja montigena Heckard, Syst. Bot. 5: 83. 1980. TYPE: U.S.A. California: San Bernardino County, N of Baldwin Lake, San Bernardino Mountains, 12 June 1976, *Heckard & Morris 4240* (holotype, JEPS; isotypes, NY, RSA, WTU).

5. *Castilleja applegatei* Fernald subsp. **pallida**

(Eastwood) Chuang & Heckard, comb. nov. Basionym: *Castilleja breweri* var. *pallida* Eastwood, Leaf. W. Bot. 2: 284. 1940. *Castilleja glandulifera* subsp. *pallida* (Eastwood) Pennell, in Abrams, Illust. Fl. Pac. States 3: 832. 1951. *Castilleja applegatei* var. *pallida* (Eastwood) N. Holmgren, Mem. New York Bot. Gard. 21: 37. 1971. TYPE: U.S.A. California: Alpine County, Carson Pass, 17 June 1940, *Eastwood & Howell 8449* (holotype, CAS; isotype, CAS).

Castilleja breweri Fernald, Erythea 6: 49. 1898. *Castilleja applegatei* var. *breweri* (Fernald) N. Holmgren in Cronquist et al., Intermountain Fl. 4: 486. 1984. TYPE: U.S.A. California: Tuolumne County, Mount Dana, 29 June 1863, *Brewer 1744* (holotype, GH; isotypes, UC, US).

Castilleja adenophora Eastwood, Leaf. W. Bot. 3: 87. 1941. TYPE: U.S.A. California: Inyo County, Mono Pass Trail, 22 July 1941, *Howell 16400* (holotype, CAS; isotypes, CAS, GH, PH, US).

6. *Castilleja applegatei* Fernald subsp. ***pinetorum*** (Fernald) Chuang & Heckard, comb. et stat. nov. *Castilleja pinetorum* Fernald, *Erythea* 6: 50. 1898. *Castilleja applegatei* var. *pinetorum* (Fernald) N. Holmgren in Cronquist et al., *Intermountain Fl.* 4: 486. 1984. TYPE: U.S.A. Oregon: Klamath County, Swan Lake Valley, 30 June 1896, *Applegate 415* (holotype, GH; isotypes, DS, PH).

Castilleja brooksii Eastwood, *Proc. Calif. Acad. Sci.* III. 2: 288. 1902. TYPE: U.S.A. California: Fresno County, Bubba Creek of King's River, 1-13 July 1899, *Eastwood s.n.* (holotype, CAS).

Castilleja trisecta Greene, *Leafl. Bot. Observ. Crit.* 1: 78. 1904. TYPE: U.S.A. California: Tulare County, Hockett's Meadow, 18 July 1904, *Baker 4431* (holotype, NDG; isotypes, CAS, GH, NY, RSA).

Castilleja pinetorum var. *fragilis* Zeile in Jepson, *Man. Fl. Pl. Calif.* 938. 1925. *Castilleja fragilis* Eastwood ex C. F. Baker, *W. Amer. Pls.* 3: 4. 1904, nomen nudum. *Castilleja applegatei* var. *fragilis* (Zeile) N. Holmgren, *Mem. New York Bot. Gard.* 21: 38. 1971. TYPE: U.S.A. California: Siskiyou County, Sisson, 14 Aug. 1903, *Copeland 3883* (holotype, CAS; isotypes, DS, GH, JEPS, MO, NY, RSA; distributed as *Castilleja fragilis*).

Castilleja excelsa Eastwood, *Leafl. W. Bot.* 2: 241. 1940. TYPE: U.S.A. California: Siskiyou County, near Spirit Lake, Marble Mountains, 4 Aug. 1939, *Howell 15058* (holotype, CAS).

Castilleja dolichostylis Eastwood, *Leafl. W. Bot.* 3: 88. 1941. TYPE: U.S.A. California: Tehama County, near Government Flat, 9 July 1941, *Eastwood & Howell 9837* (holotype, CAS; isotypes, CAS, GH, PH, US).

Castilleja wherryana Pennell, *Proc. Acad. Nat. Sci. Philadelphia* 99: 180. 1947. TYPE: U.S.A. Oregon: Baker County, Dooley Mountain, 4 July 1931, *Pennell 15454* (holotype, PH; isotypes, MO, NY, US).

Castilleja latifoliata Pennell ex Edwin, *Leafl. W. Bot.* 9: 46. 1959. TYPE: U.S.A. Nevada: Washoe County, S of Mount Ross, 24 July 1940, *Pennell 26267* (holotype, PH; isotypes, CAS, UT, UTC).

Castilleja applegatei is one of the most polytypic species of Californian *Castilleja*, but it can be distinguished from all others by its glandular-viscid herbage and usually wavy-margined leaves. Pennell (1951) recognized six species (*C. applegatei*, *C. breweri*, *C. disticha*, *C. ewanii* Eastwood, *C. gyroloba*, and *C. martinii*) in two sections of this complex, while Munz & Keck (1959) listed five (*C. applegatei*, *C. breweri*, *C. disticha*, *C. martinii*, and *C. roseana*). In his taxonomic revision of the *C. viscidula* group, Holmgren (1971) treated Californian members of the *C. applegatei* complex as comprising *C. applegatei* (with two varieties, var. *fragilis* and var. *pallida*), *C. disticha*, and *C. martinii* (with three varieties, var. *clokeyi*, var. *ewanii*, and var. *martinii*). Later, Heckard et al. (1980) added *C. montigena* from the San Bernardino Mountains of southern California, an allopolyploid

($n = 24, 36$) derived from diploid races ($n = 12$) of *C. chromosa* A. Nelson (= *C. angustifolia* (Nutt.) G. Don) and *C. martinii* var. *martinii*. The binomial *C. ewanii* has been misapplied to polyploid *C. montigena*, because the type specimen of *C. ewanii* ($n = 12$) falls within the diploid introgressants, and that name was consequently placed in synonymy under *C. chromosa* (Heckard et al., 1980).

A sufficient number of chromosome counts (Heckard, 1968; Chuang & Heckard, unpublished data) have been made in this group to show that considerable polyploidy ($n = 12, 24, 36, 48$) is present. The *C. applegatei* complex is extremely difficult taxonomically, and the complex pattern of variation has resulted in diverse treatments by earlier workers, as indicated above. The key characters used by Pennell (1951), Munz & Keck (1959), and Holmgren (1971) to identify members of this group are such differences as height of plant, degree of glandular puberulence in the herbage, leaf shape, length of corolla, and lengths of upper and lower corolla lips. In most instances, their keys allow for overlapping variation, which suggests taxonomic difficulty. It thus appears preferable to consider *C. applegatei* to be a single polytypic species. We propose the recognition of subspecies *disticha*, subspecies *martinii*, subspecies *pallida*, and subspecies *pinetorum* for the Californian members of this complex. These four subspecies can be separated imperfectly by the following key:

Key to the subspecies of *Castilleja applegatei*

- 1a. Leaves mostly 3-lobed; calyx 13-15 mm, divided ca. 1/4 on the sides; subalpine in high Sierra Nevada subsp. *pallida*
- 1b. Leaves mostly entire; calyx 12-22 mm, generally divided less than 1/4 on the sides (except some subsp. *pinetorum*); often below subalpine.
 - 2a. Calyx lobes usually obtuse to rounded; central and southern California .. subsp. *martinii*
 - 2b. Calyx lobes usually acute.
 - 3a. Calyx 12-18 mm; central and southern Sierra Nevada subsp. *disticha*
 - 3b. Calyx 16-22 mm; widespread in northern California ... subsp. *pinetorum*

7. *Castilleja hispida* Bentham subsp. ***brevilobata*** (Piper) Chuang & Heckard, comb. et stat. nov. *Castilleja brevilobata* Piper, *Proc. Biol. Sci. Wash.* 33: 104. 1920. TYPE: U.S.A. Oregon: Josephine County, 8 mi. S of Waldo, 14 June 1904, *Piper 6118* (holotype, US).

According to Ownbey (1959), *Castilleja hispida* is a common, complex, and variable species most closely related to *C. angustifolia* (= *C. chromosa*). The diploid coastal plants of northern Oregon and

the tetraploid plants of the Rocky Mountains and the Cascades of Washington are strikingly similar (Heckard, 1968). This species apparently intergrades with *C. angustifolia* and *C. miniata* where their ranges juxtapose. For example, the polyploid *C. peckiana* Pennell ($n = 36, 48, 60$; Heckard, 1968) is in fact a morphological intermediate between *C. hispida* and *C. miniata* and was reduced to synonymy under *C. miniata* (Ownbey, 1959).

When describing *C. brevilobata*, Piper (1920) allied it with *C. angustifolia*, but noted that all its parts were smaller, its leaves were shorter-lobed, and it possessed somewhat hispidulous pubescence. Holmgren (1971) placed it in the *C. viscidula* alliance because of its glandular pubescence, its somewhat crisped-margined leaves, and its geographical location. Some specimens of *C. brevilobata* are strikingly similar in habit, leaf and bract shape, and lobing pattern to *C. hispida* of coastal central and northern Oregon and Washington, except that the former exhibits glandular puberulent herbage and has a more restricted range confined to the corner of northwestern California and southwestern Oregon. Because *C. hispida* is a highly polymorphic species and none of the criteria used to separate the two is absolute, and the variation in morphological features within each group overlaps, we prefer to treat *C. brevilobata* as a subspecies of *C. hispida*.

8. *Castilleja lanata* A. Gray subsp. **hololeuca** (Greene) Chuang & Heckard, comb. et stat. nov. *Castilleja hololeuca* Greene, Pittonia 1: 39. 1887. TYPE: U.S.A. California: Santa Barbara County, Island of San Miguel, Sep. 1886, Greene s.n. (holotype, NDG; isotype, CAS).

Castilleja lanata and *C. hololeuca*, along with *C. foliolosa* Hooker & Arnott and *C. grisea* Dunkle, have been included in section *Lanatae* because of their grayish or white tomentose herbage, branched hairs, and calyx lobes, which are rounded or wholly united laterally (Pennell, 1951). *Castilleja lanata* is widespread from northern Mexico and western Texas to southern Arizona, while *C. hololeuca* is restricted to the northern Channel Islands of California. These two taxa can be distinguished by the fact that *Castilleja hololeuca* has a smaller calyx (15–18 mm) and corolla (20–25 mm). We propose to reduce *C. hololeuca* to subspecific status under *C. lanata*. *Castilleja lanata* differs from the closely related *C. foliolosa* and *C. grisea* by its white-woolly felt of long, interwoven, slightly branched hairs, and entire leaves.

9. *Castilleja minor* (A. Gray) A. Gray subsp. **spiralis** (Jepson) Chuang & Heckard, comb.

nov. Basionym: *Castilleja spiralis* Jepson, Fl. W. Mid. Calif. 412. 1901. *Castilleja stenantha* subsp. *spiralis* (Jepson) Munz, Aliso 4: 98. 1958. TYPE: U.S.A. California: Napa County, Butt's Canyon, 13 July 1897, Jepson 21113 (holotype, JEPS).

Castilleja stenantha A. Gray, Syn. Fl. N. Amer. 2: 295. 1878. TYPE: U.S.A. California: Hartweg 1897 (holotype, GH).

Castilleja minor, one of a few annual species in subgenus *Castilleja*, is widely distributed in the western United States and adjacent Mexico, growing in wet places (usually alkaline), such as marshes, streambanks, and valley hot springs. Customarily, three or four species (*C. minor*, *C. exilis* A. Nelson, *C. spiralis*, and *C. stenantha*) have been recognized in this complex. They are recognizable only by minor or very inconstant morphological features such as differences in herbage indument, length of corolla, shape of bracts, and color of lower corolla lip. Most of these characters show overlapping variation (Pennell, 1951), suggesting taxonomic difficulty. It seems preferable to treat this complex as a single variable species with two subspecies: subspecies *minor* and subspecies *spiralis*. *Castilleja minor* subsp. *minor* (including *C. exilis*) is widespread in the western United States east of the Sierra-Cascade crest and in adjacent Mexico, and is distinguished by a shorter corolla (15–20(–30) mm); in contrast, subspecies *spiralis* (including *C. stenantha*) is found only in cismontane California and has a longer corolla (25–35 cm).

10. *Castilleja subinclusa* Greene subsp. **franciscana** (Pennell) Chuang & Heckard, comb. et stat. nov. *Castilleja franciscana* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 188. 1947. TYPE: U.S.A. California: San Mateo County, Crystal Springs Lake, 15 May 1940, Pennell & Keck 25420 (holotype, PH).

Castilleja subinclusa is most closely related to *C. linariifolia* Benth. Both species share such remarkable features as an unevenly cleft calyx and a corolla generally curved forward through a calyx sinus. The calyx divides more deeply in front ($\frac{2}{3}$) than in back ($\frac{1}{6}$ – $\frac{1}{3}$), with the lobes generally curved upward. Pennell (1951) treated these two species plus *C. franciscana* Pennell in section *Linariaefoliae*. Later, Bacigalupi & Heckard (1966) described *C. jepsonii*, which is distributed in the inner South Coast Ranges from southeastern San Benito County and southward to the Sierra San Pedro Mártir in northern Baja California. They concluded that “The new species is somewhat intermediate in taxonomic

position as well as its geographic distribution between *C. affinis* and *C. linariifolia*. A hybrid origin is a possibility with the resulting hybrid derivative forming a stable self-perpetuating entity over a considerable geographic area." In that treatment, Bacigalupi & Heckard (1966) proposed to include *C. franciscana* in *C. subinclusa*. The key characters used to separate *C. subinclusa* and *C. jepsonii* comprised such variable features as color and shape of leaves, thickness of upper corolla lip, and color and shape of bract and calyx. We prefer to regard *C. subinclusa* as a highly variable species consisting of two subspecies: subspecies *subinclusa* (including *C. jepsonii*) and subspecies *franciscana*. The two subspecies can be somewhat arbitrarily distinguished by the following key.

Key to the subspecies of *Castilleja subinclusa*

- 1a. Corolla yellow-orange; calyx divided 2–4 mm on the sides, lobes clearly curved upward; Central and North Coast Ranges from Santa Cruz County north to Mendocino County subsp. *franciscana*
- 1b. Corolla reddish; calyx divided 4–7 mm on the sides, lobes barely curved upward; widespread from South Coast Ranges south to northern Baja California and central and southern Sierra Nevada foothills subsp. *subinclusa*

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